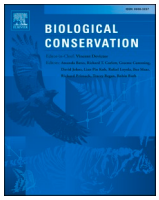
Biological Conservation 301 (2025) 110812

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Human recreation influences activity of a large carnivore in an urban landscape

Ellen C. Bolas [a,*], Adam D. Pingatore [b], Maya Mathur [c], Daniel T. Blumstein [b], Jeff A. Sikich [d], Justine A. Smith [a], John F. Benson [e], Seth P.D. Riley [b,d], Rachel V. Blakey [f,g]

[a] Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 1 Shields Avenue, Davis, CA 95616, USA
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Young Drive South, Los Angeles, CA 90095, USA
[c] Harvard Westlake High School, 700 Faring Rd, Los Angeles, CA 90077, USA
[d] National Park Service, Santa Monica Mountains National Recreation Area, 1 Baxter Way, Suite 180, Thousand Oaks, CA 91362, USA
[e] School of Natural Resources, University of Nebraska, 3310 Holdrege St., Lincoln, NE 68583, USA
[f] Biological Sciences Department, California State Polytechnic University, Pomona, 3801 W. Temple Ave, Pomona, CA 91768, USA
[g] La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California, La Kretz Hall, Los Angeles, CA 90095, USA

ARTICLE INFO

Keywords:
Mountain lion (*Puma concolor*)
Urban wildlife
Accelerometer
Diel activity
Recreation
Weekend effect

ABSTRACT

Human recreation influences the diel activity of animals and elucidating these responses informs management of species of conservation concern. We studied how mountain lions (*Puma concolor*) persisting in greater Los Angeles, California, USA adjust diel activity patterns in response to spatial and temporal variation in human recreation by combining publicly available data on recreation with GPS telemetry and accelerometer data. Mountain lions reduced diurnal activity, shifted timing of dawn activity, and became more nocturnal in areas with high recreation. There were differences in temporal responses between the sexes that might reflect behavioral shifts by females to avoid potentially dangerous male conspecifics. We found no evidence that mountain lions modified their behavior based on differences in recreation between weekdays and the weekend. The lack of a weekend effect may be a function of mountain lions being mostly nocturnal, which may be sufficient to avoid most recreation regardless of intraweek variation. Mountain lions have persisted within greater Los Angeles despite being limited spatially in this human-dominated landscape. Our work suggests that mountain lions are also constrained temporally through shifts in their diel activity.

1. Introduction

Humans impact wildlife behaviors at a global scale via recreational activities including hunting, hiking, biking, and driving vehicles (Gaynor et al., 2018; Doherty et al., 2021). As outdoor recreation grows in popularity (Larm et al., 2020), there is increasing interest in understanding the impacts of non-motorized and non-lethal recreation on wildlife behavior, in part because recreation often takes place in protected areas that serve as refuges for animals (Baker and Leberg, 2018; Anderson et al., 2023). The presence of humans causes many animals to alter their movements, space use, and patterns of diel activity where and when recreation is high (Larson et al., 2016; Lewis et al., 2021). Such behavioral adjustments may have energetic, physiological, and ultimately demographic consequences caused by altered hunting or foraging strategies or inefficient space use (Frid and Dill, 2002; Smith et al., 2017; Nickel et al., 2021), elevated stress levels (Creel et al., 2002), altered reproductive behaviors (Giese, 1996), and even local extirpation (Longshore and Thompson, 2013). Thus, understanding the impacts of recreation on wildlife behavior is essential for developing conservation and management strategies that support persistence of wildlife populations in multi-use landscapes (Baker and Leberg, 2018).

Recreation is dynamic in space and time, forcing animals to be flexible in their behavioral responses. Where recreation is spatially variable, wildlife may move to avoid areas of high human recreation (Ladle et al., 2019). In areas where there is no spatially variation in recreation but intensity is consistently high, wildlife may increase nocturnal activity (Nickel et al., 2020). Wildlife also adjust to temporal variation in recreation, as evidenced by the COVID-19 pandemic; when

* Corresponding author.
E-mail address: ebolas@ucdavis.edu (E.C. Bolas).

https://doi.org/10.1016/j.biocon.2024.110812
Received 4 July 2024; Received in revised form 3 October 2024; Accepted 6 October 2024
Available online 15 November 2024
0006-3207/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

protected areas were closed to humans during the pandemic, some species moved less or shifted timing of activity to be more diurnal (Benson et al., 2021; Anderson et al., 2023). Further, on weekends when recreation is higher as compared to weekdays, animals may avoid areas used for recreation, shift space use and foraging behavior, and change overall activity levels and timing of activity, referred to as the "weekend effect" (Stalmaster and Kaiser, 1998; Longshore and Thompson, 2013; Nix et al., 2018). Responses to recreation are thus contingent on the environmental and disturbance context, in addition to species-specific traits including habitat requirements and tolerance of people (Larson et al., 2016; Ladle et al., 2019; Lewis et al., 2021).

Globally, mammals have increased nocturnal activity in response to a wide-range of human disturbances, including recreation (Gaynor et al., 2018; Green et al., 2023). Further, in landscapes with high levels of human recreation, not only are many animals more nocturnal overall, but species that are primarily active during crepuscular times often shift to be more nocturnal (George and Crooks, 2006; Nickel et al., 2020; Lewis et al., 2021). Similarly, during times of diminished human presence or persecution, wildlife increased their diurnal activity (Anderson et al., 2023). Thus, given strong responses of animals to human impacts and the dynamic nature of human recreation, diel activity by wildlife should be plastic in response to spatiotemporal gradients of recreation.

Navigating the impacts of human recreation may be particularly demanding for large carnivores in urban areas. Recreation is likely high in and around cities because of large human populations (Nix et al., 2018) and urban landscapes are characterized by less undeveloped area overall, forcing animals to share these spaces with people and adapt to dynamic patterns of recreation. Responding to perceived risk from recreation alters essential carnivore behaviors, including space use and timing of activity (George and Crooks, 2006; Lewis et al., 2021) and cities already pose specific challenges for large carnivores, given the large space requirements, potential for conflict with humans, and aversion to humans by these species (Nisi et al., 2022). Thus as urban human populations and recreational activities grow, the conservation of urban-adjacent large carnivores and their coexistence with humans depends on understanding how they respond to spatiotemporal variation in recreation (e.g., Corradini et al., 2021).

We investigated diel activity patterns of an apex carnivore, the mountain lion (*Puma concolor*), relative to variation in human recreation in space and time in and around the megacity of Los Angeles, a metropolitan area of >18.5 million people (U.S. Census Bureau, 2015). We hypothesized that to reduce encounters with humans, mountain lions in urban areas are plastic in diel activity and respond to both spatial and temporal variation in recreation. Specifically, we analyzed accelerometer and GPS data to examine how mountain lions modified patterns of diel activity in response to variation in recreation 1) across a spatial gradient of recreation measured using the Cumulative Outdoor Activity Index (hereafter COI or recreation index), 2) temporally, between weekdays and weekends, and 3) spatially and temporally, by examining the interaction between COI and weekday/weekends. We predicted that spatial patterns of human recreation would influence diel activity of mountain lions whereby animals would be more active at night as compared to during crepuscular times, have later and earlier peaks in timing of dusk and dawn activity, spend less time active within a day, have shorter periods of inactivity, and exhibit higher rates of switching between active and inactive states in areas of high human recreation. We also expected that in response to temporal patterns of recreation, diel activity by mountain lions would show similar shifts and be most pronounced on weekends, consistent with the weekend effect. Finally, we predicted that mountain lions would respond to the interactive effects of variation in recreation in space and time and that the diel activity patterns described above would be strongest on weekends in areas of high human recreation.

2. Materials and methods

2.1. Study area

We studied mountain lions within Los Angeles and Ventura counties, California, at Santa Monica Mountains National Recreation Area (NRA), a unit of the National Park System, and surrounding areas (34°05′N, 118°46′W; Fig. 1). The study area comprised the Santa Monica Mountains, the Simi Hills, the Santa Susana Mountains, the Verdugo Mountains, and Griffith Park. Each of these patches of natural habitat were bordered by major freeways, urbanization, agricultural development, or the Pacific Ocean. The study population in the Santa Monica Mountains, in particular, has been genetically isolated from nearby populations by roads and urbanization (Riley et al., 2014; Gustafson et al., 2019), which has increased local extinction risk (Benson et al., 2016*a*). Land-use was variable across the study area, and included federal, state, and local parklands, as well as residential, urban, and agricultural areas. Natural vegetation in the study area consisted of mixed chaparral, coastal sage scrub, oak woodlands and savannas, riparian woodlands, and non-native annual grasslands. The only wild, large ungulates were mule deer (*Odocoileus hemionus*), which are the predominant prey for mountain lions in the region (Benson et al., 2016b). The climate of the study area was Mediterranean, with cool, wet winters (November–April) and hot, dry summers (May–October). The area is prone to drought and wildfire (Gillespie et al., 2018), and data were restricted to the period before a major wildfire that burned a large proportion of the study area within the Santa Monica Mountains and Simi Hills (The Woolsey Fire, 8 November 2018).

2.2. Mountain lion capture

We captured and fitted combined global positioning system (GPS) and accelerometer (activity monitor) collars to mountain lions as part of a long-term study conducted by the National Park Service (2002-present; Riley et al., 2021). During this study, we captured mountain lions using foot cable-restraints (i.e., Aldrich foot snares), baited cage-traps, or by treeing them with trained hounds. We immobilized mountain lions with ketamine hydrochloride combined with medetomidine hydrochloride, administered intramuscularly. We estimated age at capture based on body size and tooth wear measurements. For the time period analyzed in this paper, we deployed Vectronic Aerospace GPS collars (Berlin, Germany; Vertex Plus and Lite models) equipped with VHF beacons on subadult (independent animals prior to reproduction: females 14–25 months, males 14–42 months) and adult (breeding animals: females >25 months, males >42 months) mountain lions. Animal capture and handling procedures were permitted through a scientific collecting permit with the California Department of Fish and Wildlife (SCP # 05636) and the National Park Service Institutional Animal Care and Use Committee (Protocol PWR_SAMO_Riley_Mt.Lion_2014.A3). For this study, we used location and activity data for 22 individual mountain lions, collected over a 7.5-year period between 2011 and 2018. We tracked 9 females (4 adults, 2 subadults) and 13 males (4 adults, 6 subadults), with 6 individuals tracked as both subadults and adults (3 females and 3 males; Supplementary Material, Fig. S1).

Fix schedules varied, but we programmed most collars to collect eight locations per 24-h period (seven at night, one during the day). The seven fixes at night were at 2-h intervals beginning at 17:00 Pacific Standard Time (PST), and the day location was collected at 13:00 PST. On average, 95 % of programmed fixes for the time period used in this study were successful, with individual mountain lion fix rates ranging from 70 % to 100 %. Collars also collected activity data on two axes (X: anterior-posterior/surge, Y: lateral/sway), averaged across every 5-min period. Activity measurements were 99 % successful on average. Prior to analysis, we standardized activity measurements by dividing all values for separate individuals and collars by the maximum recorded value during the period the collar was worn by the animal, given collar

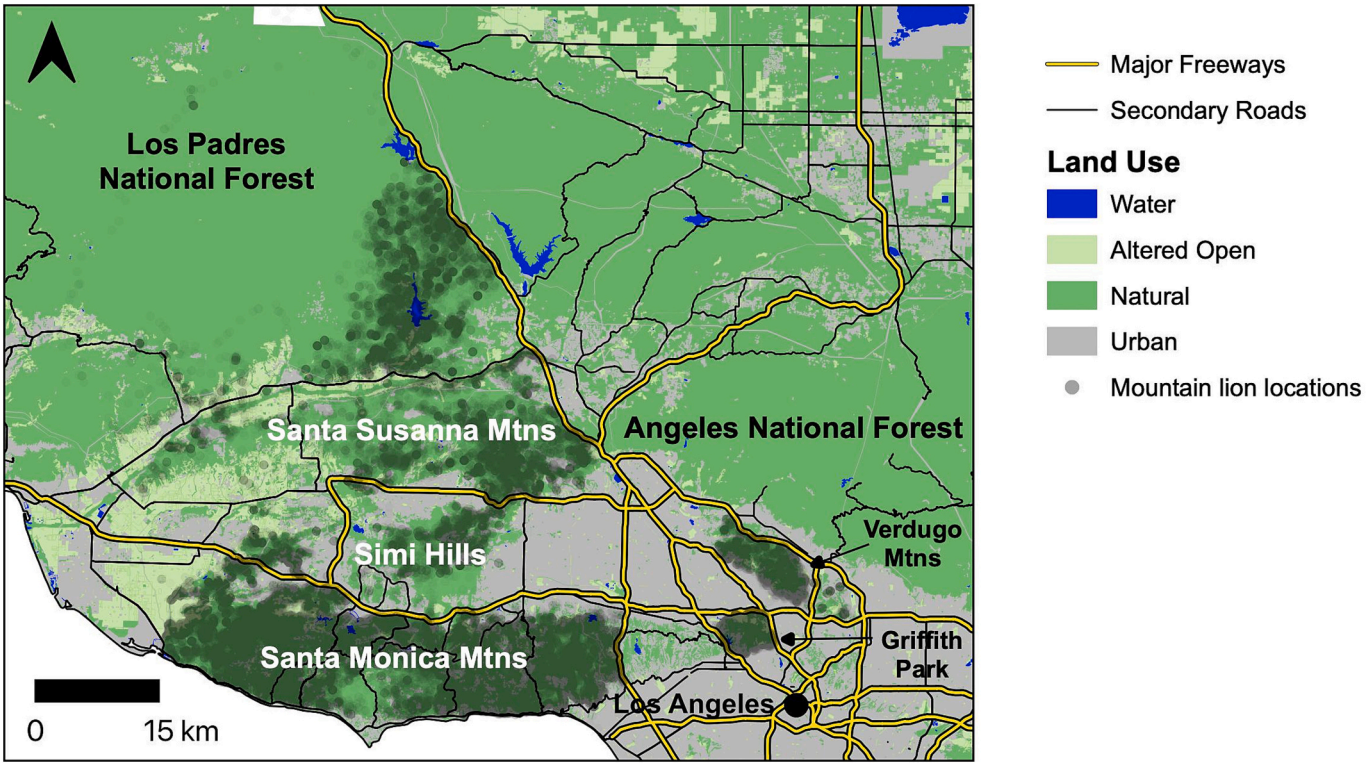


Fig. 1. Locations of all mountain lions (n = 28 individual profiles from 22 individual animals; Supplementary Material, Fig. S2) tracked during the study from 7 March 2011 to 5 October 2018 at Santa Monica Mountains National Recreation Area, California, USA.

tightness can affect acceleration values measured by the sensor (Hetem et al., 2019).

2.3. Metrics of mountain lion diel activity

We used two approaches to characterize diel activity by mountain lions: generalized additive models (GAMs) to characterize variability in activity over the diel period (i.e., 24-h) and hidden Markov models (HMMs) to characterize periods of activity and inactivity.

We used GAMs to estimate three activity metrics: a crepuscularity index, which quantified how likely an animal was to be active during crepuscular times as compared to nocturnal times, peak time of dawn activity (peak dawn activity), and peak time of dusk activity (peak dusk activity; Table 1). We used the mean of the standardized activity for each axis (X and Y) of the collar activity data, as these axes were highly correlated (R = 0.93). We fit a GAM to the activity data for each full week of each individual profile, which provided the basis from which to extract the three response variables of diel activity for each week that an animal was tracked (individual profiles = 28, models = 2289, mean weeks per individual profile = 82 ± 13 SE; Fig. 2A). We used cyclic cubic regression splines to model the relationship between activity and time of day because this approach allows for periodic (circular) variables (Wood, 2017). We fit the models beginning at midnight and beginning at midday to ensure the start time did not produce different results. The predicted activity from the two start times were highly correlated (Pearson's correlation coefficient, R > 0.99), therefore we used models starting and ending at midnight. To select the basis dimension (k) for the splines, we visually examined relationships fit with k values of 10, 12, 15, 20 and 30 (Supplementary Material, Fig. S1). The complexity of the relationship remained fairly consistent using k values ≥15, so we used k = 30 to fit all models as a precautionary measure (Wood, 2017). We used the generalized cross validation criterion to automatically estimate smoothing parameters for each model (Wood, 2017) and used the *mgcv v1.8–40* package for all GAM-fitting (Wood, 2001). To estimate peaks in

Table 1
Metrics of mountain lion diel activity, including method of calculation.

Activity metric	Description	Method
Crepuscularity Index	Index measure from −1 (completely nocturnal) to +1 (completely crepuscular)	The difference between the peak activity during crepuscular periods and the peak activity during the nocturnal period, divided by the sum of these two peak activity values.
Peak Dawn Activity (hours)	Peak in time of dawn activity, in hours before sunrise	Time of peak activity within the dawn crepuscular period (one hour before sunrise until one hour after sunrise), expressed as hours before sunrise.
Peak Dusk Activity (hours)	Peak in time of dusk activity, in hours after sunset	Time of peak activity within the dusk crepuscular period (one hour before sunset until one hour after sunset), expressed as hours after sunset.
Proportion of Day Active	Proportion of time within a day an individual was active	The number of 5-min periods assigned to the active state, divided by the number of 5-min periods assigned to the inactive state during the daytime.
Mean Inactive Period (minutes)	Mean length of a period of inactivity within a day	The mean of lengths (in minutes) of uninterrupted runs in 5-min periods assigned to the inactive state during the daytime.
Activity State Switches	Number of times an individual switched between active or inactive state within a day	The count of uninterrupted runs in 5-min periods assigned to either inactive or active state during the daytime, minus one.

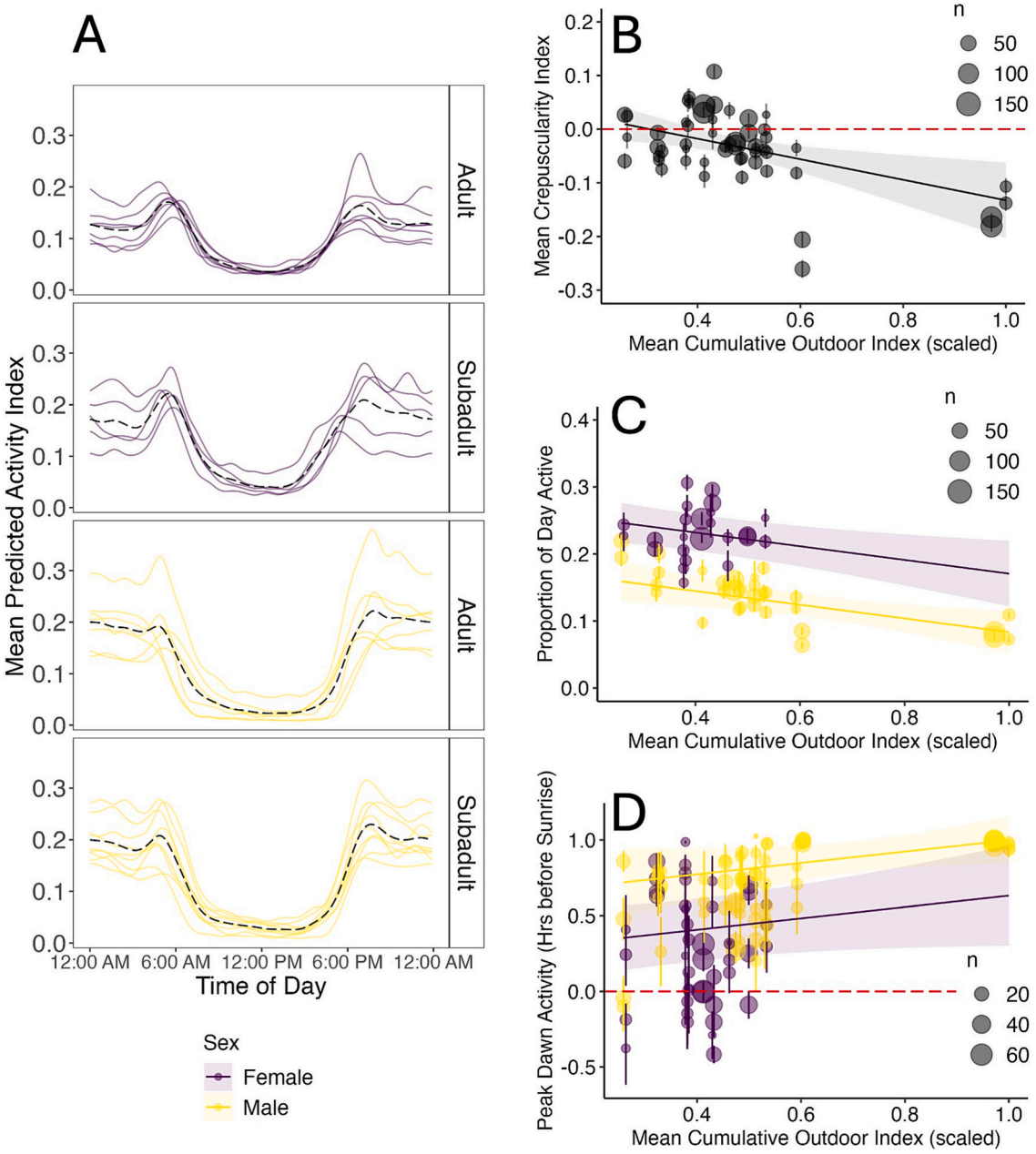


Fig. 2. Summary of mountain lion activity findings. (A) Mean diel activity for the 24-h period starting at 12 am for 22 individual mountain lions (9 females and 13 males; some individuals were tracked during both subadult and adulthood) tracked during the period from 7 March 2011 to 5 October 2018 at Santa Monica Mountains National Recreation Area, California, USA (Supplementary Material, Fig. S2). Bold dashed lines show mean relationships for each sex and age class. (B-D) Top models of the relationship between three activity metrics and a spatial gradient of human recreational activity (mean Cumulative Outdoor Index [COI]) for individual mountain lions ($n = 28$ individual profiles from 22 individual animals). (B) Relationship between crepuscularity index (i.e., how likely an animal was to be active during crepuscular times as compared to nocturnal times) and COI. A value of 1 reflects an animal that was completely crepuscular (no activity during the night) and a value of −1 reflects an animal that is completely nocturnal (no activity during crepuscular periods). (C) Relationship between proportion of time within a day an individual was active, COI, and sex. (D) Relationship between peak dawn activity, COI, and sex. Lines and shaded ribbons show fitted relationships and 95 % confidence intervals. Points show means of observed data (mean values for each individual profile in each season), and bars are standard errors.

timing of activity from the GAMs, we first converted the time of peak activity to a fraction (by dividing the time from midnight in minutes by the 1440 min in a day), then found the sunrise/sunset time for the middle day of that week (Thursday) and converted it to a fraction. We calculated the crepuscularity index as the difference between the peak activity during crepuscular periods and the peak activity during the nocturnal period, divided by the sum of these two peak activity values (Table 1). To estimate peak dawn activity, we subtracted the peak time of dawn activity from the sunrise time so that we had positive values for times that were longer before sunrise and negative values for times of peak activity after sunrise. We estimated peak dusk activity in the same way, using sunset time, so that peak times of activity after sunset had positive values and peak times before sunset had negative values. The weekly GAMs allowed us to estimate metrics of diel activity as predicted by spatial variation in human recreation. To measure how diel activity was influenced by temporal variation in recreation, we used a similar approach but calculated two sets of metrics per week: a weekday metric (Tuesday 6:00 PM to Thursday 6:00 PM PST) and a weekend metric (Friday 6:00 PM to Sunday 6:00 PM PST).

We used hidden Markov models (HMMs) to classify each mountain

lion as being either "active" or "inactive" at 5-min intervals and estimated three additional activity metrics during the day (i.e., from one hour after sunrise to one hour before sunset): the proportion of time within a day that individual mountain lions were active (proportion of day active), the mean length of a period of inactivity within a day (mean inactive period), and the number of switches between active and inactive states per day (activity state switches; Table 1). For analysis of activity data, for mountain lions that were tracked over both subadult and adulthood, we parsed the data into individual profiles by age class. Thus, of 22 animals, six individuals were tracked over both age classes, resulting in a total dataset of 28 individual profiles. Given that we did not have field observations to inform our estimations of behavioral state, we used unsupervised HMMs to estimate two states approximating "active" and "inactive" behavior (Leos-Barajas et al., 2017; see Supplementary Material for further details). Metrics of mountain lion diel activity were not highly correlated ($|R| < 0.6$; Table S1), except for proportion of day active and mean inactive period ($R = -0.75$).

2.4. Metrics of human recreation in space and time

We quantified human recreation in space using the Cumulative Outdoor activity Index (COI) based on methods from Corradini et al. (2021). The COI metric uses human activity data from the Strava Global Heatmap (Strava, 2021), which is a crowdsourced, global database of GPS-tracked recreational activities (i.e., hiking, running, cycling) that users update to be made public. Instead of measuring human presence based on structural proxies like infrastructure, COI provides a direct estimate of recreation on an annual scale from individual humans on the landscape (Corradini et al., 2021; see Supplementary Material for further details). We estimated the area of space used by each individual mountain lion and age class using local convex hulls (LoCoH), a method that performs well when animal movement is constrained by barriers like roads and urban areas (Getz et al., 2007). We used the *adehabitatHR v0.4.16* package (Calenge, 2006) to fit adaptive LoCoHs, where the "a" parameter used the maximum number of nearest neighbors because all those points were within the maximum distance between any two points in the dataset. We then took mean estimates of the COI across the space used by each mountain lion during the period for which we were measuring diel activity (Supplementary Material, Fig. S2). This resulted in 28 measurements of COI, one for each individual profile. The annual average number of visitors to Santa Monica Mountains NRA was consistent across our study period, giving us confidence in using these COI estimates in this way (see Supplementary Material for further details).

To measure temporal variation in recreation, we used periods encompassing the weekend (Friday 6:00 pm PST to Sunday 6:00 pm PST), representing times when we expected higher levels of human recreation, and weekday (Tuesday 6:00 pm PST to Thursday 6:00 pm PST), representing times when we expected relatively lower levels of human recreation. We separated weekend and weekday into two-day periods to measure the same length of time for both, to reduce autocorrelation in movement between the two time periods, and to avoid periods when people may occasionally take "long weekends" (e.g. Fridays and Mondays). These time periods are consistent with 2018 reports from visitor surveys within Santa Monica Mountains NRA where 75 % of survey respondents reported visiting the park on weekends compared to 37 % on weekdays and visitors spent nine more minutes in the park on weekends compared to weekdays (UCLA Luskin Center for Innovation, 2020).

2.5. Analyzing the influence of spatial variation in human recreation

We used a mixed-effects meta-regression approach to model the relationships between each metric of diel activity metric (crepuscularity index, peak dawn activity, peak dusk activity, proportion of day active, mean inactive period, activity state switches) and COI separately. Mixed effects meta-regression accounts for the uncertainty in estimates of mean metrics of diel activity and weights means within the analysis based on sample sizes. We therefore took the mean and variance for each individual profile in each season (total = 56) as the effect sizes (*yi*) and sampling variance (*vi*). We included individual profile as a random intercept and COI, sex, age class, and season as moderators (predictors). We assessed model fit and parsimony using an information theoretic approach to compare models, allowing us to account for variability among sexes, age-classes, and seasons (Supplementary Material, Table S2). We ranked and compared models in two stages using Akaike's Information Criterion for small samples sizes (AICc; Burnham and Anderson, 1998). For each stage, we considered the model with the lowest AICc to be the most strongly supported, and when multiple models were within <2 AICc of the top model, we interpreted the simplest (least number of parameters) model. For the first stage, we compared models containing human recreation (COI) and additional descriptors of individual animals (sex and age class) to the null model. We then checked the top-ranked model from the first stage to evaluate whether adding season (wet and dry) improved model fit (Table S2). We used the *metafor v. 3.4–0* package to fit all meta-regression models (Viechtbauer, 2010) and used the *MuMIn v.1.46.0* package to compare models (Bartoń, 2022).

2.6. Analyzing the influence of temporal variation in human recreation

We used the dataset of weekday and weekend metrics of diel activity for this analysis, and used the mean, variance, and sample size (number of weeks) for both weekend and weekday periods for each week and each individual profile, to estimate the effect size (*yi*), as the log response ratio:

$$yi = log\left(\frac{\overline{X}_{weekend}}{\overline{X}_{weekday}}\right)$$

Where $\overline{X}_{weekend}$ is the mean of all weekend measurements for a given metric, and $\overline{X}_{weekday}$ is the mean of all weekday measurements for a given metric. The sample variance was then estimated as per Hedges et al. (1999):

$$vi = \frac{SD^2_{weekend}}{n_{weekend}\overline{X}^2_{weekend}} + \frac{SD^2_{weekday}}{n_{weekday}\overline{X}^2_{weekday}}$$

Where $SD^2_{weekend}$ and $SD^2_{weekday}$ are the standard deviations for the weekend and weekday measurements and $n_{weekend}$ and $n_{weekday}$ are the sample sizes (number of weeks). The log response ratio is centered around 0 where positive values indicate the measured metric has a higher value on the weekend, whereas negative values indicate the metric has a higher value on weekdays. We therefore refer to the effect size of each metric as "the weekend effect of" that metric.

We used a meta-analytic approach to assess whether mountain lion diel activity varied between weekdays and weekends, as a proxy for temporal variability in human presence. We again fit mixed-effects meta-regression models, with individual profile as a random intercept. To test whether there was a difference in diel activity between weekdays and weekends (i.e., the weekend effect), we built a full set of models that included moderators of sex, age class, and season (Supplementary Material, Table S2). We included an intercept-only (null) model which was a test of global weekend effect, independent of other factors. We used model comparison, as explained above, and considered the model with the lowest AICc to be the most strongly supported (Supplementary Material, Table S3). We also used a z-test to assess whether effect sizes of weekend as compared to weekday were different from zero for each metric in the intercept-only model (Supplementary Material, Tables S3 & S5).

2.7. Analyzing the influence of the interaction in spatial and temporal variation in human recreation

We used the models with the strongest support in predicting the weekend effect from the previous step and added COI as a linear and quadratic moderator to test for a linear or curvilinear relationship between the weekend effect of each metric of diel activity and COI, which would indicate an influence of human recreation in both space and time on mountain lion diel activity. We used model comparison with AICc, as explained above, to assess whether these predictors explained further variability (Supplementary Material, Tables S2 & S3).

2.8. Model validation

The most parsimonious models were validated (except where the null model was retained) by running 1000 iterations of the model, with 10 % of the dataset removed each time (Supplementary Material, Fig. S3).

3. Results

3.1. Influence of spatial variation in human recreation on mountain lion activity

The level of recreation in our study area (as measured with COI) ranged from 0.26 to 1.0. COI was retained in the most strongly supported models for every activity metric except for peak time of dusk activity (Table 2). The highest levels of COI (~1) were measured within Griffith Park (Fig. 1), which is a highly urban park featuring trails, concert venues, and a zoo within 1740 ha. The lowest COI was measured in the Santa Susana Mountains and the Los Padres National Forest, areas with limited human access and infrastructure (Fig. 1).

The crepuscularity index was strongly influenced by COI (−0.19, 95 % CI = −0.32 to −0.06; Fig. 2B, Table 2; Supplementary Material, Table S4, Fig. S3), indicating that in areas of higher human recreation, mountain lions shifted their diel activity to become more nocturnal. The most crepuscular individual in the study had a mean crepuscularity index of 0.11 (more crepuscular) and the least crepuscular individual had a crepuscularity index of −0.26 (more nocturnal).

The proportion of time during a day (from one hour after sunrise to one hour before sunset) that mountain lions were active was also strongly influenced by COI (−0.1, 95 % CI = −0.17 to −0.03; Fig. 2C, Table 2; Supplementary Material, Table S4, Fig. S3), meaning that in areas of higher recreation, mountain lions spent less time active during daylight hours. Female mountain lions were overall more active during the day than males. Mountain lions spent 25 % (females) and 15 % (males) of the day active in areas with low recreation and 17 % (females) and 8 % (males) of the day active in areas of high recreation.

We found marginal support for the prediction that COI influenced peak time of dawn activity (0.38, 95 % CI = −0.05 to 0.81), mean length of period of inactivity within a day (64.46, 95 % CI = −0.55 to 129.5), and the number of switches in activity state within a day (3.46, 95 % CI = −2.37 to 9.28; Fig. 2D, Table 2; Supplementary Material, Table S4, Figs. S3-S5). The fitted relationship for peak time of dawn activity for female mountain lions ranged from 21 min before sunrise in areas of low recreation to 38 min before sunrise near higher recreation, and timing of activity for males ranged from 43 min before sunrise around low recreation to an hour before sunrise in areas of higher recreation. While the mean length of a period of inactivity during the day varied with sex, age, and growing season, across all groups the mean period of inactivity was 48 min longer in areas with high COIs as compared to low COIs. The number of times a mountain lion switched between active and inactive state varied with sex, age, and growing season. Across all groups, individuals switched between activity states 2.6 more times in high COI areas than in low COI areas.

We found no evidence that human recreation influenced peak time of dusk activity, as the top model was the null model (Table 2; Supplementary Material, S4).

Table 2
Spatial gradients in recreation – Model comparison from mixed-effects meta-regression models analyzing how a spatial gradient of human recreation influences diel activity of mountain lions (n = 28 individual profiles from 22 individual animals) in Santa Monica Mountains National Recreation Area, California, USA. Models were ranked and compared using AICc. Model comparison was done in two stages: the first stage compared models containing human recreational activity (COI) and additional descriptors of mountain lion individuals (sex and age class), and the second stage took the top model from the first stage and added season.

Activity metric	Formula	df	AICc	ΔAICc	Weight
Crepuscularity Index	~ COI + Sex	4	−157.23	0	0.44
	~ COI	3	−156.98	0.25	0.39
	~ 1	2	−153.64	3.59	0.07
	~ COI + COI^2	4	−151.72	5.51	0.03
	~ COI + Sex + Age	5	−151.65	5.58	0.03
	~ COI + Age	4	−151.25	5.99	0.02
	~ Season (wet, dry) + COI	4	−151.05	6.19	0.02
	~ COI + Sex * Age	6	−145.61	11.63	<0.01
Peak Dawn Activity	~ COI + Sex	4	39.08	0	0.43
	~ COI + Sex + Age	5	40.39	1.32	0.22
	~ Season (wet, dry) + Sex + COI	5	41.33	2.26	0.14
	~ COI + Sex * Age	6	42.53	3.45	0.08
	~ COI	3	42.91	3.84	0.06
	~ COI + Age	4	44.35	5.27	0.03
	~ COI + COI^2	4	44.41	5.33	0.03
	~ 1	2	48.66	9.58	<0.01
Peak Dusk Activity	~ 1	2	−14.41	0	0.69
	~ COI + Sex	4	−11	3.41	0.13
	~ COI	3	−9.66	4.76	0.06
	~ Season (wet, dry)	3	−9.3	5.12	0.05
	~ COI + Sex * Age	6	−7.88	6.53	0.03
	~ COI + COI^2	4	−7.35	7.06	0.02
	~ COI + Sex + Age	5	−6.42	7.99	0.01
	~ COI + Age	4	−5.42	8.99	0.01
Proportion of Day Active	~ COI + Sex	4	−170.35	0	0.92
	~ COI + Sex + Age	5	−165.28	5.07	0.07
	~ COI + Sex * Age	6	−159.06	11.28	<0.01
	~ COI	3	−155.97	14.38	<0.01
	~ COI + COI^2	4	−151.05	19.3	<0.01
	~ Season (wet, dry) + COI + Sex	4	−150.79	19.55	<0.01
	~ COI + Age	4	−150.64	19.70	<0.01
	~ 1	2	−149.83	20.51	<0.01
Mean Inactive Period	~ Season (wet, dry) + COI + Sex * Age	7	490.84	0	0.95
	~ COI + Sex * Age	6	496.78	5.94	0.05
	~ COI + Sex + Age	5	503.39	12.55	<0.01
	~ COI + Sex	4	511.69	20.85	<0.01
	~ COI + Age	4	527.77	36.93	<0.01
	~ COI + COI^2	4	529.01	38.17	<0.01
	~ COI	3	536.19	45.35	<0.01
	~ 1	2	550.10	59.26	<0.01
Activity State Switches	~ Season (wet, dry) + COI + Sex * Age	7	258.73	0	0.76
	~ COI + Sex * Age	6	261.50	2.77	0.19
	~ COI + Sex + Age	5	264.88	6.15	0.04
	~ COI + Sex	4	266.98	8.25	0.01
	~ COI + Age	4	275.90	17.17	<0.01
	~ COI + COI^2	4	278.33	19.59	<0.01
	~ COI	3	281.00	22.26	<0.01
	~ 1	2	283.74	25.00	<0.01

3.2. Influence of temporal and spatial variation in human recreation on mountain lion activity

We did not find evidence that shifts in recreation between weekdays and weekends influences diel activity for mountain lions. The null model was the top model for each activity metric in the model comparison, and when testing the global effect of the weekend effect on each metric, all

intercept coefficients were $\leq |0.03|$and crossed zero (Supplementary Material, Tables S3 & S5). We found no evidence that human recreation in space (COI) increased or decreased the strength of the weekend effect in any of the diel activity metrics measured for mountain lions, as the null model was the top model for each set of model comparisons (Supplementary Material, Table S3).

4. Discussion

Wildlife often employ antipredator behaviors in response to human activities, even when such activities do not present a lethal threat (Frid and Dill, 2002; Smith et al., 2021, 2024; Lasky and Bombaci, 2023). When available, animals may select areas of lower human activity that are perceived as less risky. However, animals in highly modified landscapes may have limited options to avoid humans and instead alter their activity patterns to avoid times of high human activity (Frid and Dill, 2002). In densely populated areas of southern California, natural areas are heavily used by recreationists, limiting the ability of mountain lions to shift to landscapes with lower recreation overall; thus, it is not surprising that we found evidence of mountain lions altering diel activity in response to spatial variation in recreation.

As predicted, mountain lions in and around Los Angeles were more nocturnal and less crepuscular in areas of high recreational activity. The relationship between nocturnality and recreation was largely driven by two adult male mountain lions, P22 and P41, who lived in the most urban portions of the study area (Riley et al., 2021). Mountain lion P41 was the most nocturnal animal in our study area and occupied the Verdugo Mountains, a small range bounded by freeways and intense development, with high levels of recreation (COI = 0.60) that likely influenced his activity patterns. Mountain lion P22 was the second-most nocturnal animal and occupied the area with the highest levels of recreation in our study (COI = 0.97 [adult]), with a home range in Griffith Park surrounded by freeways and densely populated neighborhoods within the city of Los Angeles. It is interesting that these two mountain lions were the most nocturnal and apparently the most sensitized to humans, as we might have expected the opposite pattern, where animals in highly urban areas would become more habituated to humans (Uchida et al., 2019) and be less likely to shift their diel activity. However, habituation by carnivores may increase potential for conflict with humans and mortality risk (White and Gehrt, 2009; Shimozuru et al., 2020). Hence, the retention of fear of humans by urban carnivores and individual abilities to alter activities in time (this study) or space to avoid humans (Reilly et al., 2022) may be an important adaptive response to enable co-occurrence with humans. The least nocturnal mountain lion was P13, who had COI levels of 0.43 in her home range in the central and western portion of the Santa Monica Mountains. Given that mountain lions are typically active at night, the shift away from crepuscular activity may be an easy means of responding to the diurnal nature of human recreation, and is a pattern that has been identified in other nocturnal and crepuscular species (George and Crooks, 2006; Lewis et al., 2021; Lasky and Bombaci, 2023).

We also found that mountain lions were less active during daylight and found marginal support for longer periods of inactivity during daylight hours when near areas of high recreation. Mountain lions with home ranges in areas with high recreation were inactive for approximately one more hour of the day as compared to individuals in areas of low recreation. Our finding contrast with Wang et al. (2017), who found that mountain lions in the Santa Cruz Mountains were more active overall in developed areas, likely because they switched more frequently between active and inactive states as compared to mountain lions in more remote areas. Animals must spend a minimum amount of time active every diel period to forage, travel, defend themselves, and rest, but when already functioning at a minimum threshold, may shift timing of activity rather than overall amount of activity (Lendrum et al., 2017). The overall similarity in the amount of the diurnal periods that mountain lions in and around Los Angeles were active may reflect that they have already reduced the amount of time they are active and are at their minimum threshold of activity, such that recreation has little influence on the overall amount of time they spend active. It is likely that mountain lions in our study are therefore using nighttime activity to help meet energetic needs.

Interestingly, female and male mountain lions showed differences in responses to recreation, as females were more active during the day and were active closer to sunrise than males. Male mountain lions are a source of mortality for females and dependent kittens (Riley et al., 2014; Benson et al., 2020), and females in this system show evidence of avoiding habitats used by males (Benson et al., 2016b). Diel activity of female mountain lions may be constrained by avoiding males such that they do not exhibit as strong of a response to humans.

Counter to our predictions, mountain lions in our study did not appear to alter diel activity on weekends, even when in areas of high recreation. Our findings are consistent with other studies where the weekend effect does not hold for nocturnal species due to limited overlap with recreation in a 24-h period (Nix et al., 2018; Lewis et al., 2021; Green et al., 2023). Further, we suspect that in Los Angeles, a highly urban city, mountain lions may have developed a level of tolerance for the presence of human recreation (Uchida et al., 2019). Additionally, mountain lions have large home ranges, so because they adjust their activity to spatial variation in human recreation (as demonstrated in our study) they may not be sensitive to certain locations within their home ranges having higher risk at specific times. Questions remain about how individual variability in factors like diet, space use, and overall exposure to humans may contribute to the impact of the weekend effect.

Mountain lions showed phenotypic plasticity in their behavioral responses to recreation, however, the costs of this plasticity to their fitness are unknown. Perceiving humans as a threat is essential for survival as humans are the main source of mortality for mountain lions across California (Benson et al., 2023), and around Los Angeles, vehicle strikes are the most common cause of mountain lion mortality (Benson et al., 2020). However, by treating recreating humans as a source of risk and modifying their behavior as a result, mountain lions may experience increased energetic or opportunity costs, as predicted by risk-foraging theory (Smith et al., 2021, 2024). Mountain lions have large energy requirements and experience challenges when hunting in developed landscapes, therefore changes to diel activity may compound the negative impacts of human disturbance on energy budgets (Wang et al., 2017; Nickel et al., 2021). While some of the shifts in diel activity that we measured appeared to be small (i.e., in areas of high human recreation, mountain lions changed timing of peak dawn activity by an average of 17 min), alterations to activity patterns for these mountain lions occur within the context of contending with several other stressors concurrently, including moving through densely populated neighborhoods, crossing busy freeways and roads, and exposure to poisons (Benson et al., 2020). Thus, recreation impacts on mountain lions may be experienced as a cumulative stressor for this population, potentially impacting individual physiology, movement, or hunting (Nickel et al., 2021; Robertson et al., 2023; Smith et al., 2024). For example, in response to a fire that burned 70 % of the Santa Monica Mountains and Simi Hills, mountain lions increased space use and distance traveled, likely expending more energy as a result, and were more active during daylight hours (Blakey et al., 2022). However, several mountain lions in and around Los Angeles, including P41 and P22, lived for a long time in areas with high recreation and high development, so plasticity in diel activity alone is unlikely to limit survival for individuals in this population and likely enhances their ability to coexist with humans.

Many studies of urban carnivores focus on human-induced challenges such as habitat loss, infrastructure development, and lethal interactions. Our results add to a growing body of literature which shows that sub-lethal interactions with recreationists lead to behavioral alterations in wildlife (Larson et al., 2016; Lasky and Bombaci, 2023), with the potential to intensify the effects of urbanization. Our findings

present both conservation challenges and reasons for optimism as natural areas around cities strive to provide protected habitat for wildlife and offer recreation opportunities for people. A key component to addressing these challenges is the extent to which plasticity in diel activity in response to recreation results in demographic or fitness consequences for wildlife. By building on our study and behavioral and energetic modeling (e.g., Nickel et al., 2021), future studies can investigate whether mountain lions incur fitness costs from avoiding humans in space and time in human-dominated landscapes. Additionally, combining knowledge of adjustments in diel activity by individual mountain lions with understanding of fine-scale habitat use relative to variation in recreation may reveal strategies that enable animals to persist in areas that are heavily impacted by humans. Further, this information can support protection of mountain lions and humans by identifying key locations and times that serve as refuges for mountain lions. In Los Angeles, all mountain lions experience some level of recreation on a regular basis and are proactively altering diel activity to avoid overlap with recreating humans, a behavior which may play an important role in minimizing conflict.

CRediT authorship contribution statement

Ellen C. Bolas: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Adam D. Pingatore:** Writing – original draft, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maya Mathur:** Methodology, Investigation, Data curation, Conceptualization. **Daniel T. Blumstein:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Jeff A. Sikich:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Justine A. Smith:** Writing – review & editing, Writing – original draft, Methodology. **John F. Benson:** Writing – review & editing, Writing – original draft, Methodology. **Seth P.D. Riley:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Rachel V. Blakey:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to have conducted research for this project on the traditional, ancestral, and unceded territory of the Tongva, Gabrielino (eno/eño)/Tongva, Chumash, Kizh and Tatavium peoples. Our authors further acknowledge that they have worked on this project as guests on the lands of the Patwin, Pawnee, Oto-Missouria peoples, and the shared lands of many other tribes. We thank National Park Service biologists JG Moriarty and JL Brown as well as the many dedicated field volunteers, interns, and technicians who assisted with this research. We thank the La Kretz Center for California Conservation at UCLA and the National Park Foundation for funding RVB's work on the project. ECB was supported by the NSF GRFP, the NSF INTERN, and the UC Davis Gradate Group in Ecology Fellowship.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110812.

Data availability

Data supporting this research are sensitive and not available publicaly, contact Santa Monica Mountains National Recreation Area for more information.

References

Anderson, A.K., Waller, J.S., Thornton, D.H., 2023. Partial COVID-19 closure of a national park reveals negative influence of low-impact recreation on wildlife spatiotemporal ecology. Sci. Rep. 13, 1–11. https://doi.org/10.1038/s41598-023-27670-9.

Baker, A.D., Leberg, P.L., 2018. Impacts of human recreation on carnivores in protected areas. PloS One 13, e0195436. https://doi.org/10.1371/journal.pone.0195436.

Bartoń, K., 2022. MuMIn: multi-model inference. R package version 1.47.1. https://CRAN.R-project.org/package=MuMIn.

Benson, J.F., Mahoney, P.J., Sikich, J.A., Serieys, L.E.K., Pollinger, J.P., Ernest, H.B., Riley, S.P.D., 2016a. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proc. R. Soc. B Biol. Sci. 283, 20160957. http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2016.0957.

Benson, J.F., Sikich, J.A., Riley, S.P.D., 2016b. Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban-wildland gradient. PloS One 11, e0158006. https://doi.org/10.1371/journal.pone.0158006.

Benson, J.F., Sikich, J.A., Riley, S.P.D., 2020. Survival and competing mortality risks of mountain lions in a major metropolitan area. Biol. Conserv. 241, 108294. https://doi.org/10.1016/j.biocon.2019.108294.

Benson, J.F., Abernathy, H.N., Sikich, J.A., Riley, S.P.D., 2021. Mountain lions reduce movement, increase efficiency during the Covid-19 shutdown. Ecol. Solutions Evidence 2, e12093. https://doi.org/10.1002/2688-8319.1209.

Benson, J.F., Dougherty, K.D., Boyce, W.M., Cristescu, B., Gammons, D.J., Garcelon, D. K., Higley, J.M., Martins, Q.E., Nisi, A.C., Riley, S.P.D., Sikich, J.A., Stephenson, T. R., Vickers, W.T., Wengert, G.M., Wilmers, C.C., Wittmer, H.U., Dellinger, J.A., 2023. The ecology of human-caused mortality for a protected large carnivore. Proc. Natl. Acad. Sci. 120, e2220030120. http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2216830120/-/DCSupplemental.doi:10.1073/pnas.2216830120.

Blakey, R.V., Sikich, J.A., Blumstein, D.T., Riley, S.P.D., 2022. Mountain lions avoid burned areas and increase risky behavior after wildfire in a fragmented urban landscape. Curr. Biol. 32, 4762–4768 e5. https://doi.org/10.1016/j.cub.2022.08.082.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag New York, Inc.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Corradini, A., Randles, M., Pedrotti, L., van Loon, E., Passoni, G., Oberosler, V., Rovero, F., Tattoni, C., Ciolli, M., Cagnacci, F., 2021. Effects of cumulated outdoor activity on wildlife habitat use. Biol. Conserv. 253, 108818. https://doi.org/10.1016/j.biocon.2020.108818.

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B., Peterson, R.O., 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv. Biol. 16, 809–814. https://doi.org/10.1046/j.1523-1739.2002.00554.x.

Doherty, T.S., Hays, G.C., Driscoll, D.A., 2021. Human disturbance causes widespread disruption of animal movement. Nat. Ecol. Evol. 5, 513–519. https://doi.org/10.1038/s41559-020-01380-1.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Ecol. Soc. 6, 11. http://www.consecol.org/vol6/iss1/art11/.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360, 1232–1235. https://doi.org/10.1126/science.aar7121.

George, S.L., Crooks, K.R., 2006. Recreation and large mammal activity in an urban nature reserve. Biol. Conserv. 133, 107–117. https://doi.org/10.1016/j.biocon.2006.05.024.

Getz, W.M., Fortmann-roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., Wilmers, C.C., 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PloS One 2, e207. https://doi.org/10.1371/journal.pone.0000207.

Giese, M., 1996. Effect of human activity on adelie penguin Pygoscelis adeliae breeding success. Biol. Conserv. 75, 157–164. https://ui.adsabs.harvard.edu/link_gateway/1996BCons..75..157G/doi:10.1016/0006-3207(95)00060-7.

Gillespie, T.W., Ostermann-Kelm, S., Dong, C., Willis, K.S., Okin, G.S., MacDonald, G.M., 2018. Monitoring changes of NDVI in protected areas of southern California. Ecol. Indic. 88, 485–494. https://doi.org/10.1016/j.ecolind.2018.01.031.

Green, A.M., Young, E., Keller, H., Grace, T., Pendergast, M.E., Sekercioglu, C.H., 2023. Variation in human diel activity patterns mediates periodic increases in recreational activity on mammal behavioural response: investigating the presence of a temporal 'weekend effect.'. Anim. Behav. 198, 117–129. https://doi.org/10.1016/j.anbehav.2023.02.002.

Gustafson, K.D., Gagne, R.B., Vickers, T.W., Riley, S.P.D., Wilmers, C.C., Bleich, V.C., Pierce, B.M., Kenyon, M., Drazenovich, T.L., Sikich, J.A., Boyce, W.M., Ernest, H.B., 2019. Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conserv. Genet. 20, 215–227. https://doi.org/10.1007/s10592-018-1125-0.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2.

Hetem, R.S., Mitchell, D., De Witt, B.A., Fick, L.G., Maloney, S.K., Meyer, L.C.R., Fuller, A., 2019. Body temperature, activity patterns and hunting in free-living cheetah: biologging reveals new insights. Integr. Zool. 14, 30–47. https://doi.org/10.1111/1749-4877.12341.

Ladle, A., Avgar, T., Wheatley, M., Stenhouse, G.B., Nielsen, S.E., Boyce, M.S., 2019. Grizzly bear response to spatio-temporal variability in human recreational activity. J. Appl. Ecol. 56, 375–386. https://doi.org/10.1111/1365-2664.13277.

Larm, M., Erlandsson, R., Norén, K., Angerbjörn, A., 2020. Fitness effects of ecotourism on an endangered carnivore. Anim. Conserv. 23, 386–395. https://doi.org/10.1111/acv.12548.

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PloS One 11, e0167259. https://doi.org/10.1371/journal.pone.0167259.

Lasky, M., Bombaci, S., 2023. Human-induced fear in wildlife: a review. J. Nat. Conserv. 74, 126448. https://doi.org/10.1016/j.jnc.2023.126448.

Lendrum, P.E., Crooks, K.R., Wittemyer, G., 2017. Changes in circadian activity patterns of a wildlife community post high-intensity energy development. J. Mammal. 98, 1265–1271. https://doi.org/10.1093/jmammal/gyx097.

Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T.A., Watanabe, Y.Y., Murgatroyd, M., Papastamatiou, Y.P., 2017. Analysis of animal accelerometer data using hidden Markov models. Methods Ecol. Evol. 8, 161–173. https://doi.org/10.1111/2041-210X.12657.

Lewis, J.S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A.R., VandeWoude, S., Crooks, K.R., 2021. Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. Ecosphere 12, e03487. https://doi.org/10.1002/ecs2.3487.

Longshore, K., Thompson, D.B., 2013. Detecting short-term responses to weekend recreation activity: desert bighorn sheep avoidance of hiking trails. Wildl. Soc. Bull. 37, 698–706. https://doi.org/10.1002/wsb.349.

Nickel, B.A., Suraci, J.P., Allen, M.L., Wilmers, C.C., 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biol. Conserv. 241, 108383. https://doi.org/10.1016/j.biocon.2019.108383.

Nickel, B.A., Suraci, J.P., Nisi, A.C., Wilmers, C.C., 2021. Energetics and fear of humans constrain the spatial ecology of pumas. Proc. Natl. Acad. Sci. 118, e2004592118. https://doi.org/10.1073/pnas.2004592118.

Nisi, A.C., Benson, J.F., Wilmers, C.C., 2022. Puma responses to unreliable human cues suggest an ecological trap in a fragmented landscape. Oikos 2022, e09051. https://doi.org/10.1111/oik.09051.

Nix, J.H., Howell, R.G., Hall, L.K., McMillan, B.R., 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: testing the weekend effect. Behav. Processes 146, 16–21. https://doi.org/10.1016/j.beproc.2017.11.002.

Reilly, C.M., Suraci, J.P., Smith, J.A., Wang, Y., Wilmers, C.C., 2022. Mesopredators retain their fear of humans across a development gradient. Behav. Ecol. 33, 428–435. https://doi.org/10.1093/beheco/arab150.

Riley, S.P.D., Serieys, L.E.K., Pollinger, J.P., Sikich, J.A., Dalbeck, L., Wayne, R.K., Ernest, H.B., 2014. Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. Curr. Biol. 24, 1989–1994. https://doi.org/10.1016/j.cub.2014.07.029.

Riley, S.P.D., Sikich, J.A., Benson, J.F., 2021. Big cats in the big City: spatial ecology of mountain lions in greater Los Angeles. J. Wildl. Manag. 85, 1527–1542. https://doi.org/10.1002/jwmg.22127.

Robertson, K.E., Ellington, E.H., Tonra, C.M., Gehrt, S.D., 2023. Stress in the city? Coyote hair cortisol varies with intrinsic and extrinsic factors within a heavily urbanized landscape. Sci. Total Environ. 901, 165965. https://doi.org/10.1016/j.scitotenv.2023.165965.

Shimozuru, M., Shirane, Y., Yamanaka, M., Nakanishi, M., Ishinazaka, T., Kasai, S., Nose, T., Shirayanagi, M., Jimbo, M., Tsuruga, H., Mano, T., Tsubota, T., 2020. Maternal human habituation enhances sons' risk of human-caused mortality in a large carnivore, brown bears. Sci. Rep. 10, 16498. https://doi.org/10.1038/s41598-020-73057-5.

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C. C., 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proc. R. Soc. B Biol. Sci. 284, 20170433. https://doi.org/10.1098/rspb.2017.0433.

Smith, J.A., Gaynor, K.M., Suraci, J.P., 2021. Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. Front. Ecol. Evol. 9, 604973. https://doi.org/10.3389/fevo.2021.604973.

Smith, J.A., McDaniels, M.E., Peacor, S.D., Bolas, E.C., Cherry, M.J., Dorn, N.J., Feldman, O.K., Kimbro, D.L., Leonhardt, E.K., Peckham, N.E., Sheriff, M.J., Gaynor, K.M., 2024. Population and community consequences of perceived risk from humans in wildlife. Ecol. Lett. 27, e14456. https://doi.org/10.1111/ele.14456.

Stalmaster, M.V., Kaiser, J.L., 1998. Effects of recreational activity on wintering bald eagles. Wildl. Monogr. 137, 3–46. http://www.jstor.org/stable/3830779.

Strava, 2021. Strava Global Heatmap. Retrieved January, 2021 from. strava.com/heatmap.

Uchida, K., Suzuki, K.K., Shimamoto, T., Yanagawa, H., Koizumi, I., 2019. Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. Behav. Ecol. 30, 1583–1590. https://doi.org/10.1093/beheco/arz117.

UCLA Luskin Center for Innovation, 2020. Results of the 2018 Visitor Survey and Visitor Count in the Santa Monica Mountains National Recreation Area. Los Angeles, California, USA.

U.S. Census Bureau, 2015. Metropolitan and micropolitan statistical area tables. Retrieved April, 2021 from. https://www.census.gov/data/tables/time-series/demo/popest/2010s-total-metro-and-micro-statistical-areas.html.

Viechtbauer, W., 2010. Conducting Meta-analyses in R with the metafor package. J. Stat. Softw. 36, 1–48. https://doi.org/10.18637/jss.v036.i03.

Wang, Y., Smith, J.A., Wilmers, C.C., 2017. Residential development alters behavior, movement, and energetics in an apex predator, the puma. PloS One 12, e0184687. https://doi.org/10.1371/journal.pone.0184687.

White, L.A., Gehrt, S.D., 2009. Coyote attacks on humans in the United States and Canada. Hum. Dimens. Wildl. 14, 419–432. https://doi.org/10.1080/10871200903055326.

Wood, S.N., 2001. Mgcv: GAMs and Generalized Ridge Regression for R. R News 1: 20–25.

Wood, S.N., 2017. Generalized Additive Models: An Introduction With R, 2nd edition. Chapman and Hall/CRC, New York, US.